

NESTS, TERRITORIES, AND REPRODUCTION OF SEDGE WRENS (*CISTOTHORUS PLATENSIS*)

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Sedge Wrens (*Cistothorus platensis*) share many features of their breeding biology with the congeneric Marsh Wren (*C. palustris*). Both species defend all-purpose territories in "grassland" habitat (Orians 1969), are highly insectivorous, and while sexually monomorphic in appearance, populations of both species may exhibit polygyny at levels ranging from 30-50% (Welter 1935; Walkinshaw 1935; Verner 1964, 1965a; Kale 1965; Crawford 1977). Males of both species build a number of domed nests which play a central role in courtship (Verner 1965a, Burns 1977). Crawford (1977) has documented the occurrence of polygyny in the Sedge Wren, but few other basic features of the social organization of this species have been reported, thus precluding valuable comparisons with the better studied Marsh Wren. This paper discusses territory characteristics, reproductive performance, parental care and mating patterns of Sedge Wrens.

STUDY AREA

The 3.3-ha study site is located in Polk County, Minnesota, 20 km east and 10 km south of Crookston. The sedge meadow used by the wrens during the 1976 season was subject to light grazing by cattle as recently as 1973, but in 1976 it appeared relatively undisturbed. Grasses (*Calamagrostis neglecta*, *C. inexpansa*) and sedges (*Scirpus acutis*, *Carex stricta*, *C. sartwellii*, *C. buxbaumii*, *C. aquatilis*) were the most abundant species. The meadow was flooded with about 20 cm of water early in May but by late July no standing water was present. Yellow Warblers (*Dendroica petechia*), Yellowthroats (*Geothlypis trichas*), Red-winged Blackbirds (*Agelaius phoeniceus*) and Swamp Sparrows (*Melospiza georgiana*) were also common in the meadow.

METHODS

Twelve males and 14 females were captured for banding by chasing them into mist nets placed in their territories and near nests. Sexes were distinguished by song and by the presence or absence of a cloacal protuberance (Salt 1954). Five males situated near observation towers ("tower males") were individually color banded; 12 of the 14 females were color banded by the time their first young fledged. Observations were made using binoculars and a spotting telescope from three 2-m high open towers and from canvas blinds located near nests. Observations were made almost daily from 12 May-11 August 1976. Watches from the towers began before sunrise and continued until males began foraging at about 07:30 (CST). Evening watches extended from about 19:00 until activity ceased after sunset. A 25-m grid of lathing helped to pinpoint male singing locations and was used to estimate territory size.

Data on parental care and foraging patterns were collected from blinds during the periods 07:30-12:00 and 16:00-20:00 in June, 09:00-12:00 and 16:00-19:00 in July and August. After

arriving in the first blind I waited 5 min for the birds to settle down and then collected data on the first 15 trips by the female. I then moved to another blind and so sampled the activities at three or four nests each morning and evening, rotating the order of observation from day-to-day. Data collected at 14 nests included: (1) distance from the nest to where foraging began, (2) kind of vegetation used for foraging, (3) whether or not the site was within the male's territory, and (4) the length of time spent at and away from the nest. Rarely could I identify what the young were being fed.

Nests were examined at least every second day. Those found during incubation were back-dated based on a 14-day incubation period (Walkinshaw 1935, Crawford 1977). Three nests were found after the young had hatched and were dated by comparing the degree of development with young of known age. Nests were located either by observing males building them or by systematic searches using a stick to brush aside the concealing vegetation. Territories were searched for nests at least once a week.

Pair bond terminology follows Martin (1974). The first female to pair with a polygynous male is a "primary" female, while subsequent mates, regardless of the extent of temporal overlap with first paired females, are "secondary" females. Nests with eggs laid in them before 1 July are "early nests"; those begun afterwards are "late nests."

RESULTS

The multiple nests built by *Cistothorus* males are used for nesting, as dormitories, and possibly as decoys for predators (Verner 1965a, Burns 1977). Those used for nesting have a substantial inner lining of grass, sedge and feathers added by females. Most courtship activities occur near nests; Verner and Engelson (1970) found a positive relationship between the number of nests built by male Marsh Wrens and the number of females to whom they were mated. The 12 male Sedge Wrens on my study area built an average of 7.4 complete nests per male (Table 1) from 17 May–11 August. Males were still building when I left in August, and since four males left in late July while the remaining males continued to build nests, I estimate that males present for the entire season build an average of about nine nests. Males left an average of 0.8 nests incomplete, consisting of only a spheroid network of sedge or grass. There were no instances of stacked nests (one built on top of another) nor of nests built in localized "courting centers" (Fig. 1), both of which have been reported for Marsh Wrens (Verner 1965a, Verner and Engelson 1970).

I found no significant relationship (Spearman Rank Correlation) between the number of nests built in each territory and (a) territory size, or (b) amounts of the major vegetation types (*Scirpus acutis*, *Carex stricta*, *C. aquatilis*). Polygynous males built eight, seven, and seven nests each, suggesting no clear relationship between the ability to attract second mates and the number of nests built. The sample sizes are too small, however, to support conclusions in this regard.

Territory size.—Sedge Wren territories are used for courting, nesting and much of the foraging. The territories presented in Fig. 1 represent

TABLE 1
TERRITORY SIZE, COMPOSITION AND NUMBER OF NESTS BUILT BY 12 MALE SEDGE WRENS

Male	Territory size (m ²) ^a	Amount major vegetation (m ²) ^b	% major vegetation	No. of nests
B	1589	1225	82	8
R	1274	970	76	8
G	1777	1402	79	5
Y	1486	853	57	9
BB	2106	1580	75	8
M54	1592	902	57	13
M62	1844	1242	70	7
M63	3559	501	14	5
M66	1287	597	46	6
M67	1586	1008	63	6
M69	1570	615	39	7
M71	1695	1057	62	7
\bar{x}	1780	996	60	7.4

^a Based on territories of the week 9 July–15 July.

^b Major vegetation includes *Scirpus acutis-Carex stricta-C. aquatilis*, and monotypic patches of *C. aquatilis*.

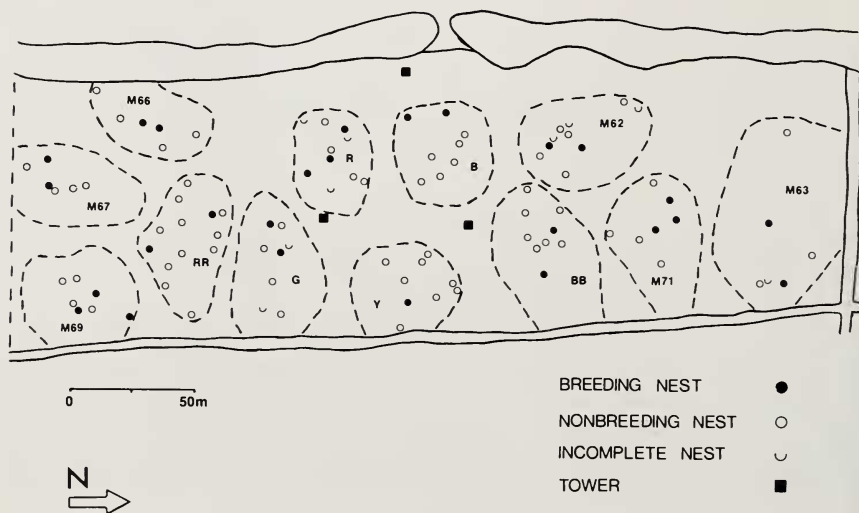


FIG. 1. Territories of 12 male Sedge Wrens during the week beginning 9 July, when most females were beginning their second clutches.

“maximum” areas of males (Odum and Kuenzler 1955, Stenger and Falls 1959), determined by plotting the positions of males while singing during the week beginning 9 July and taking the largest perimeter. All new positions were recorded, rather than plotting positions at constant intervals (Odum and Kuenzler 1955) or at each sighting (Stenger and Falls 1959). The average territory size of the 12 males was 1780 m² (Table 1). Territory sizes of the five tower males were estimated separately for 8 consecutive weeks, based on about 20 h of observation per week. Seasonal maximum territories were constructed by superimposing the eight weekly estimates for each male and taking the largest perimeter, yielding an average seasonal maximum territory size of 2259 m². The grand mean, 1280 m², an average of the 40 estimates obtained for the five males, is considerably less than that obtained by superimposing the weekly territories. Thus, males tended to stop defending some portions of their territories and shifted to new areas as the season progressed.

Reproduction.—Females began laying on or about the third day of nest-lining, after which one egg was laid each day. Incubation began before clutches were complete, as hatching extended over a 2- or 3-day period. Only females incubated. The incubation period, from the laying of the last egg to hatching of the last egg, was normally 14 days (six of seven nests with all eggs hatching). The overall nesting success (number of nests producing at least one young/number of initiated clutches) was high (69%), as expected for a passerine species laying in an enclosed nest (Nice 1957), and was similar to that reported by Crawford (1977) for a sample of 31 nests (68%). Nest failures in my study were due to predation (five) or infertile clutches (two). One of the five nests whose contents were thought to have been preyed on may instead have been destroyed by another wren (see Picman 1977a, 1977b).

Apparently females in some populations of Sedge Wrens are double-brooded (a second clutch of eggs is produced after young from the first nest fledge), whereas females in other populations are not. Walkinshaw (1935) suggested that Sedge Wrens are double-brooded, based on records of very late nesting dates, whereas Crawford (1977) found that none of the females he studied renested after producing young. In the population I studied most of the successful females laid additional clutches (Fig. 2), but with interesting exceptions. Three of the 12 males were paired to two different females during the season. In two of these cases the primary female did not reneest, while in the third case the female did reneest but after pairing to a male on a different territory. Monogamous and primary females began their nests within a week of each other, on the average, while primary and secondary females differed by about one and a half months. Late nests of previously successful monogamous females were begun at nearly the same time as were the first nests of secondary females.

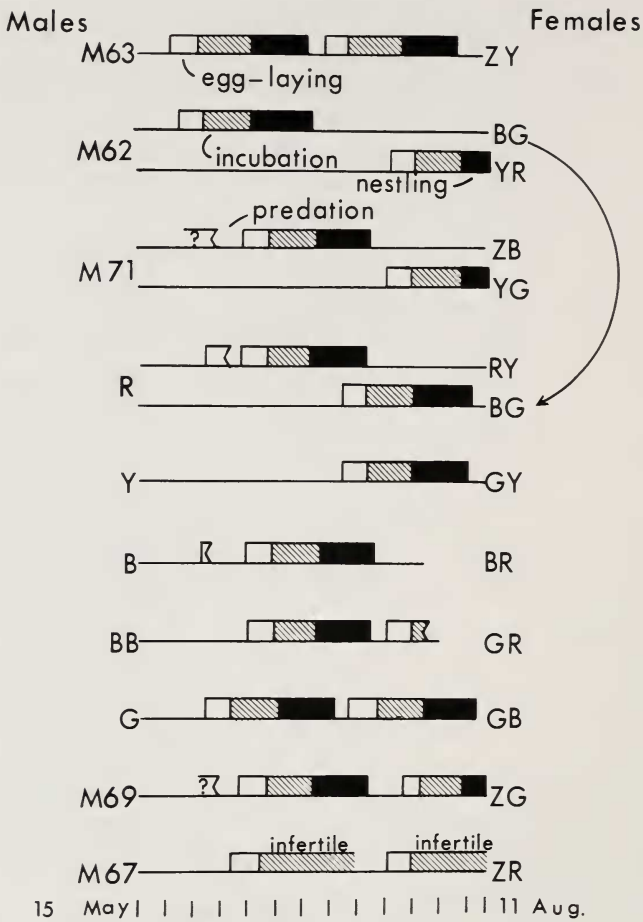


FIG. 2. Nesting schedule of Sedge Wrens over weekly intervals. Clutch initiation dates for two destroyed nests are unknown and are indicated by question marks. The reproductive activities in one other territory were similar to those shown for BB's territory, while events in a second unrepresented territory resembled those in M63's.

All first clutches of monogamous and primary females found prior to hatching contained seven eggs (Table 2), the clutch-size suggested by Bent (1948). Clutch-sizes of late nests of monogamous females were more variable (4-7) and were significantly smaller than first clutches ($t = 4.54$, $P < 0.001$). Secondary females laid slightly larger clutches ($\bar{x} = 6.0$) than did late nesting monogamous females ($\bar{x} = 5.7$), but the sample sizes are small. Monogamous females fledged significantly fewer young late in the season than they did earlier ($t = 6.06$, $P < 0.001$) and about the same

TABLE 2
CLUTCH-SIZE AND FLEDGING SUCCESS OF EARLY^a AND LATE NESTING FEMALE SEDGE
WRENS

Pairing status	Clutch-size		Young produced		Fledging success	
	Early	Late	Early	Late	Early	Late
Monogamous	7.0 (5) ^b	5.7 (8)	5.1 (6)	3.4 (5)	0.72 (6)	0.56 (5)
Primary	7.0 (2)	—	5.3 (3)	—	0.75 (3)	—
Secondary	—	6.0 (3)	—	3.3 (3)	—	0.55 (3)

^a Early nests were those initiated before 1 July 1976.

^b Sample sizes are in parentheses.

number as did secondary females nesting at the same time (Table 2). Overall, the fledging success (number of young fledged per number of eggs laid, including only nests from which at least one young fledged) was 0.67, but again seasonal differences occurred. Early nests of monogamous females averaged 0.72 young per egg laid, while late in the season these same females fledged 0.56 young per egg laid. Secondary females had a fledging success of 0.55 young per egg laid.

Average differences between the reproductive success of monogamous and polygynous males were the result of a higher rate of nest failure for monogamous males. Monogamous males produced an average of 5.9 young during the season, while polygynous males averaged 8.6 young. This difference resulted largely from predation on the late nests of monogamous males and the two infertile clutches of M67. If only monogamous males that successfully produced young from both early and late nests are considered, monogamous males average 8.5 young ($N = 4$).

Parental care.—Table 3, based on 98 h of observation at 14 nests, summarizes feeding schedules for 1976. All but three nests were observed from at least day 4 to day 10 (average nestling age; day of hatching is day 0). Most males continued to advertize for females and build nests during the nestling period, and consequently provided little food for nestlings. While six of the nine males observed were recorded bringing food to nestlings, only three males contributed 10% or more of the nestlings' food (based on number of trips). The extent of male parental care was similar for first and second broods of monogamous females and for the single broods of primary and secondary females. There did not appear to be a correlation between the number of young fledged and the extent of male parental care.

As with Marsh Wrens and other passerine species (Verner 1965a, Royama 1966, Martin 1974) Sedge Wrens tend to feed nestlings more fre-

TABLE 3
PROVISIONING OF NESTLINGS BY ADULT SEDGE WRENS

Male	Female	Total trips	Trips by male	Young fledged
R	RY (early)	187	2	6
	BG (late)	141	1	3
M71	ZB (early)	51	18	6
	YG (late)	89	0	4
M62	BG (early)	71	11	4
	YR (late)	58	13	3
G	GB (early)	163	0	5
	GB (late) ^a	154	0	4
M64	ZG (early)	110	0	6
	ZG (late)	33	0	3
Y	GY (late)	193	86	3
BB	GR (early)	102	0	5
M54	RG (early)	107	10	5
M66	YB (early)	52	3	4
Total		1511	144	

^a Male G disappeared after female GB completed laying her second clutch.

quently as the nestlings age. Females also fed similarly-aged young at significantly higher rates later in the season than earlier (Wilcoxon Ranked Pairs Sign Test, $P < 0.01$), as Gibb (1950) also found for two species of parids. No clear tendency for males to increase their feeding rates was found, possibly because of the low levels at which they were sampled.

DISCUSSION

Because of the small sample sizes involved, comparisons of the reproductive success of monogamous, primary and secondary females must be made cautiously. Nonetheless, certain trends appear to exist. Secondary females nested much later in the season than did primary females, with no temporal overlap within territories in two of three cases. Monogamous females present for the entire season showed a significant seasonal decrease in both clutch-size and number of young fledged. Because females paired to monogamous males often were double-brooded, while females paired to polygynous males were single-brooded (on my study area), the data suggest that females paired to monogamous males were most successful for the entire season (fledging 5.8 young per female, compared to

5.3 young for primary and 3.3 young for secondary females). It seems likely that several of the females I studied (e.g., YR, YG, GY; Fig. 2) were reproductively active off of my study area, making comparisons of seasonal reproductive success invalid. Primary females produced on average more young than did secondary females, but this may largely be a result of differences in nesting time and a general pattern of clutch-size reduction during the season. Neither primary nor secondary females differed substantially from monogamous females nesting at the same time.

The Orians-Verner-Willson model (Orians 1969, 1972; Verner and Willson 1966, 1969) and more recent amendments to the original model (Wittenberger 1976, 1979; Altman et al. 1977) deal primarily with species in which primary and secondary females share, in time, the resources available in a male's territory. Both food (Willson 1966) and nest-sites (Willson 1966, Holm 1973, Best 1977) have been indicated as critically distributed resources, such that males defending territories with abundant food and/or nest-sites are more likely to attract more than one female. This abundance theoretically compensates nesting primary and secondary females for the probable loss of male parental care, either in feeding young or defending young from predators.

The Orians-Verner-Willson hypothesis may also apply to species in which the nesting activities of primary and secondary females do not overlap, although there should perhaps be a change in emphasis away from food availability. Male parental care in this situation need not be reduced, and in habitats such as marshes where insects emerging throughout the season prevent depletion of food resources in territories, secondary females may not be subject to a reduction in food availability. In such situations variations in nest-site quality or availability may be the principal factor on which females base their choice of territories. Sedge Wren females do appear to choose their territories, at least in part, on the basis of the degree of protection from predators the vegetation offers. That polygynous males defended better nest-sites late in the season is suggested by the different rates of predation in the territories of monogamous and polygynous males. Predators (and possibly other wrens) destroyed none of the three late nests of polygynous males, while two of the eight nests of monogamous males were disrupted.

Intraspecific comparisons.—Two key differences exist between the population of Sedge Wrens studied by Crawford (1977) and the population reported on here. First, renesting by successful females did not occur in the population Crawford studied; second, Crawford found significant temporal overlap of the nesting activities of primary and secondary females paired to the same male. Various authors (Meanley 1952, Sherman 1952, Kroodsmas and Verner 1978) have been impressed by the Sedge Wren's

opportunistic breeding strategy. Times of arrival vary substantially at a site from one year to the next. Birds present at a location in May can disappear by July, and the first arrivals in an area can be as late as mid-July (Meanley 1952, Sherman 1952, pers. obs.). During the 1976 season 12 males were present in the meadow, which I used for my study, early in the season. The following year only two males were present, neither of them banded, although laying had begun. Within a single breeding season males and females may abruptly appear or disappear from a meadow (Fig. 2). In short, Sedge Wrens are characterized by high mobility during the breeding season and low site tenacity between seasons. This opportunistic behavior may have selected for unique features in the communication system of Sedge Wrens (Kroodsmma and Verner 1978) and therefore is presumably not of recent origin (say in response to agriculture). This opportunism adds another dimension of variability between populations, and may explain differences between populations of Sedge Wrens studied to date.

Interspecific comparisons.—Considerable variation occurs between populations of Marsh Wrens studied to date, probably due to gross differences in climate and habitat. The migratory habits of a population (resident or migrant) may be one factor influencing the social organization of a species (cf. Orians 1961, 1973; Verner 1965a) and therefore I will restrict my comparisons to the migratory eastern Washington Marsh Wrens studied by Verner (1965a) and Verner and Engelson (1970).

Male Sedge Wrens build about half as many nests as do Marsh Wrens (9 and 20, respectively), in territories that are 5–6 times as large (1800 and 300 m², respectively). Polygyny is present at approximately the same frequency in both species, with about one-third of the breeding males having more than one mate, but the overlapping of the nesting activities of primary and secondary females is more pronounced in Marsh Wrens. Several cases of trigamy have been reported for Marsh Wrens (Welter 1935; Verner 1964, 1965a), but none as yet has been recorded for Sedge Wrens. Both Sedge and Marsh wren females frequently renest after fledging young, and in neither species do males provide substantial amounts of parental care.

Most of these differences may be due to differences in food availability. Territories of Marsh Wrens vary substantially in average size from one population to another, variation suggested by Verner (1965a) to be a result of differences in food availability. An extension of his argument may be sufficient to explain the larger territories of Sedge Wrens. Orians (1980) discusses a general east to west trend of increasing secondary aquatic productivity, a trend possibly reflected interspecifically in territory size. Other differences, especially the greater amount of temporal overlap of

nesting primary and secondary female Marsh Wrens and the greater number of nests built by Marsh Wrens may also be explained by higher levels of food availability in the territories of Marsh Wrens, but this is largely conjecture.

Clearly what is needed to understand the quantitative differences between the two species is comparative information on time budgets, prey biomass per unit area and the nutritive values of utilized prey. Much of this information has already been obtained for Marsh Wrens (Kale 1965, Verner 1965b), and while the task of obtaining accurate time budget data on Sedge Wrens seems formidable, it would provide key information on the evolution of *Cistothorus* social systems.

SUMMARY

Twelve male Sedge Wrens (*Cistothorus platensis*) defended all-purpose territories averaging 1780 m², building an estimated average of nine nests each. Three of the males were polygynous. The mates of six monogamous males renested after successfully fledging young. Because of second nesting attempts, monogamous females averaged the highest fledgling success (5.8 young), followed by primary (5.3 young) and secondary (3.3 young) females. A seasonal decrease in clutch-size of monogamous females (from 7.0–5.7), combined with within season arrivals and departures of females confounds the analysis of reproductive success. Little difference was found between the success of different classes of females nesting at the same time. Polygynous males nonetheless achieved a higher mean reproductive success than did monogamous males, largely due to higher rates of predation on the late nests of monogamous males.

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